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River flow, substrate type and *Hydrurus* density as major determinants of macroinvertebrate abundance, composition and distribution

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Introduction

It is generally accepted that numerous factors including temperature, flow, substrate, aquatic and riparian vegetation, dissolved substances, food, biotic interactions and watershed influences determine the composition and abundance of stream benthos. Among these factors, temperature, flow and substrate are considered major factors controlling benthic macroinvertebrate life (Hynes 1970, Ward & Stanford 1979). A study of a mountain stream in the Austrian crystalline alps extended over a period of more than two years has provided an opportunity to discuss the distributional patterns of the macrozoobenthic community of a scarcely documented area in relation to different substrates and streamflow conditions.

Study site

The Wagrainer Ache is an epi- to metarhithral, 4th-order crystalline subalpine stream with a nival hydrographic regime (Keller 1961). The stream drains a 142.5 km^2 area of the Central Alps and flows into the Salzach River, a main tributary of the Inn-Danube-system. The study site is located between the villages of Wagrain and St. Johann in the province of Salzburg at about 700 m a.s.l. (47°20′N lat., 13°30′E long.). Within the sampled area, the Wagrainer Ache runs off through a shaded V-shaped valley. The surrounding area is covered by a coniferous dominated (mainly *Picea abies*) mixed woodland. The stream's width ranges between 7 and 21 m, with a mean width of 12.1 m. The substrate consists mainly of three choriotop-types (nomenclature according to Steffan (1965), Braukmann (1987), Moog (1989): Megalithal: Boulders having more than 40 cm diameter, rocky areas, 29 % area of stream bottom. Lithal: Cobbles, with various shares of gravel and sand, 61 %. Psammal and akal: Sand and gravel, 10 %. The stream's mean discharge is 4.7 $m^3 \cdot s^{-1}$. The calculated mean current velocities of a given profile are 1.0 $m \cdot s^{-1}$, at average annual flow conditions, and 0.53 $m \cdot s^{-1}$, at average annual low flow conditions. During normal water flows, with spates excluded, the effective current velocities range between 0 and 0.3 $m \cdot s^{-1}$ above psammal areas, between 0.4 and 1.8 $m \cdot s^{-1}$ above lithal areas and between 0.5 and 3.0 $m \cdot s^{-1}$ above megalithal areas. The hydrochemical parameters measured (Table 1) characterize the Wagrainer Ache as a well oxygenated, and moderately nutrient polluted stream.

Table 1. Mean annual concentrations of hydrochemical parameters 1984–1986 (with standard deviation and numbers of sampling dates).

Parameter (unit)	Mean	SDEV	Number
pH units	8.42	0.53	64
Conductivity ($\mu S \cdot cm^{-1}$ 25°)	274	88.5	116
Alkalinity (mval)	1.71	0.22	21
Dissolved oxygen ($mg \cdot l^{-1}$)	12.5	1.30	30
Total phosphorus ($mgP \cdot m^3$)	74	51	114
Total nitrogen ($mg\ N \cdot m^3$)	750	350	51
(83 % NO_3–N, 11 % NH_4–N, 0.8 % NO_2–N, 5 % N_{org})			

Methodology

Benthos was collected from riffles with a modified Surber (box type) sampler (1000 cm^2 sampling area, 112 μm mesh size). Sampling was done to a sediment depth of at least 30 cm. The surface of rocky areas or those with boulders was sampled with a Surber sampler which had a thick foam flange around its bottom to ensure a proper seal. Drift samples were taken primarily with a drift net. The vertical distribution of the benthic animals in lithal sediments was studied with the help of a modified Stocker-Williams-N_2-freezing corer. For a detailed description of this sampling gear, see Bretschko & Klemens (1986). Because of the more economically employable Surber sampler, the catching efficiency of this sampling gear was compared with the N_2-freezing corer. At two sites located about two km from each other, similar to one another due to the hydraulic and morphometric characteristics, but of a different shading degree, samples were taken. The faunal abundances collected showed no differences in the catching efficiency of the two sampling gears used (Table 2).

The good coincidence of the catching efficiencies of both sampling gears is in contradiction to the results obtained by other authors (e.g. Kroger 1972), who found that the Surber sampler underestimated the quantity of benthic macroinvertebrates. Two explanations for the

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Table 2. Comparison of catching efficiency of Surber sampler and N_2-freeze corer (t-Test, 5 replicates each, means with 95 % confidence intervals, individual-abundance per 1000 cm^2, calculated after a log (x + 1) transformation).

	Site 1		Site 2	
	Surber	Freeze-corer	Surber	Freeze-corer
Mean + C.L.	1850	2400	1130	1200
Mean	1210	1270	780	850
Mean – C.L.	790	675	540	600
Calculated value of t		0.181		0.387
Tabulated value of t		2.262		2.262

good sampling results of the Surber sampler can be given. First, the modified gear prevented the escape of benthic animals and sampling was done to a sediment depth of (minimal) 30 cm. Second, as was detected with the help of the freeze-corer, most of the benthic fauna of the Wagrainer Ache were vertically distributed within the upper 30 cm. Because the gear was easier to handle and because of economical reasons, the Surber-sampler was preferred.

Sampling was conducted monthly except during flood periods. At least 4 replicates were taken from each habitat at each site: Altogether 570 quantitative benthic samples were taken. Samples were processed in 4 % formalin. At the laboratory, the organisms were separated, identified to the lowest determinable taxonomic level, counted and weighed. For weight determination, the fresh weight was determined, using filter paper to remove the liquid film.

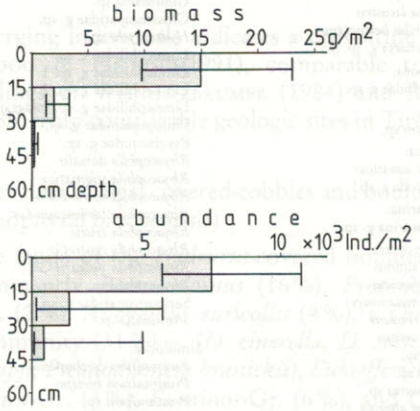

Fig. 1. Benthic vertical distribution (total biomass and total abundance). Thin bars indicate 95 % confidence limits, calculated after a log (x + 1) transformation.

Results and discussion

Vertical distribution

As the aim of the study was to describe quantitatively the seasonal and spatial distribution of the benthic animals, sampling gear had to be chosen which could fulfill the goals of the study by means of economically feasible conditions. According to the results of Hynes et al. (1974), verified for Austrian rivers by Bretschko (1981), which show a distinct depth distribution of single organisms with maxima between 20 to 60 cm, the vertical distribution of the benthic animals in the Wagrainer Ache was studied in order to be able to choose the right gear for lithal sampling.

Five samples each from 2 sites were taken with the freeze-corer. To characterize the vertical distribution, the sampled core was separated into four portions, each of 15 cm length. The results show that 99 % of the benthic faunal biomass and 95 % of the individual numbers are distributed within the upper 30 cm of the sediment (Fig. 1). The reported depth distribution indicates that the benthic fauna is obviously restricted to a layer nearer the surface. An analysis of the grain size distribution from these cores indicates a clogging of the deeper interstitial caverns with sediment particles of small grain sizes (Frauendorfer 1987). No colonizeable sediment layers could be detected in depths below 40–50 cm. The fact that the bed sediments of crystalline brooks are of a lower porosity than those reported for calcareous brooks (Bretschko 1981) explains the discrepancy of the vertical distribution values reported for rivers with calcareous catchments.

Taxonomic composition of benthic invertebrates

During the investigation time (March 1984–October 1986), a total of 314 taxa could be recorded (Table 3). The choriotope with the greatest species richness was the lithal, with 229 taxa recorded, followed by the megalithal areas, with 139 taxa, and the akal-psammal zones, with 107 taxa (Table 4). Out of 187 taxa found in drift samples

Table 3.

Turbellaria:
Turbellaria g. sp. 1
Nematomorpha:
Gordius aquaticus
Gordius sp.
Mermithoidea g. sp.
Oligochaeta:
Eiseniella tetraedra
Enchytraeidae g. sp.
Haplotaris gordioides
Lumbricidae g. sp.
Lumbriculidae g. sp. 1
Marionina sp.
Naididae g. sp.
Oligochaeta g. sp.
Pristina sp.
Stylaria lacustris
Stylodrilus heringianus
Oligochaeta g. sp. juv.
Gastropoda:
Planorbidae g. sp.
Bivalvia:
Pisidium sp.
Crustacea:
Asellus aquaticus
Ostracoda g. sp.
Hydracarina:
Hydracarina g. sp.
Ephemeroptera:
Baetis alpinus
Baetis fuscatus
Baetis melanonyx
Baetis rhodani
Baetis vernus
Baetis sp.
Caenis sp.
Ecdyonurus sp.
Epeorus alpicola
Ephemerella major
Habroleptoides modesta
Rhithrogena hybrida
Rhithrogena hybrida Gr.
Rhithrogena loyolaea-Gr.
Rhithrogena semicolorata Gr.
Rhithrogena sp.
Plecoptera:
Amphinemura sp.
Brachyptera risi
Brachyptera seticornis
Brachyptera sp.
Capnia bifrons
Capnia nigra
Capnia vidua
Capnia sp.
Chloroperla tripunctata
Chloroperla sp.
Dictyogenus alpinus
Dictyogenus fontium
Dictyogenus sp.
Isoperla cf. grammatica
Isoperla grammatica
Isoperla sp.
Leuctra braueri
Leuctra cingulata
Leuctra fusca
Leuctra inermis
Leuctra nortoni
Leuctra prima
Leuctra sp.
Nemoura nortoni
Nemoura sp.
Perla marginata
Perla grandis
Perla sp.
Perlodes intricatus
Perlodes sp.
Perlodidae juvenil
Protonemura cf. *lateralis*
Protonemura cf. nimborus
Protonemura hrabei
Protonemura lateralis
Protonemura nitida
Protonemura sp.
Rhabdiopteryx alpina
Rhabdiopteryx sp.
Taeniopteryx schoenemundi
Coleoptera:
Elmis rietscheli
Elmis sp.
Hydraena sp.
Limnius sp.
Trichoptera:
Allogamus auricollis
Allogamus sp.
Drusus discolor Gr.
Ecclisopteryx guttulata
Glossosoma sp.
Glossosomatidae g. sp.
Hydropsyche sp.
Limnephilidae g. sp.
Limnephilidae g. sp. 1
Limnephilidae g. sp. 2
Limnephilidae g. sp. (magrain)
Philopotamidae g. sp.
Psychomidae g. sp.
Rhyacophila dorsalis
Rhyacophila stigmatica
Rhyacophila torrentium
Rhyacophila torrentium-Gr.
Rhyacophila tristis
Rhyacophila tristis-Gr.
Rhyacophila vulgaris-Gr.
Rhyacophila sp.
Sericostomatidae g. sp.
Vormaldia sp.
Simuliidae:
Eusimulium carthusiense
Prosimulium hirtipes
Prosimulium sp.
Simulium argyreatum
Simulium monticola
Simulium reptans
Simulium variegatum
Simulium sp.
Simuliidae g. sp.
Chironomidae:
Boreoheptagyia sp.
Brillia longifurca
Brillia modesta
Brillia sp.
Bryophaenocladius sp.
Cardiocladius capucinus
Cardiocladius fuscus
Cardiocladius sp.
Chaetocladius Gen. sp.
Chaetocladius cf. *dentif.*
Chaetocladius dentiforceps-Gr.
Chaetocladius perennis
Chaetocladius piger-Gr.
Chaetocladius piger
Chaetocladius sp.
Chaetocladius vitellinus-Gr.
Chironomini Gen. sp.
Chironomus plumosus-Gr.
Conchapelopia sp.
Corynoneura cf. *lacustris*
Corynoneura cf. *lobata*
Corynoneura lobata
Corynoneura scutellata-Gr.
Corynoneura scutellata
Corynoneura sp.
Cricotopus annulator
Cricotopus cf. *annulator*
Cricotopus annulator/curtus
Cricotopus fuscus
Cricotopus intersectus
Cricotopus tremulus
Cricotopus tremulus-Gr.
Cricotopus cf. *triannulatus*
Cricotopus trifascia
Cricotopus sp.
Cyphomella cornea
Diamesa cf. *bertrami*
Diamesa cinerella
Diamesa cinerella-Gr.
Diamesa ciner.-zernyi-Gr.
Diamesa dampfi
Diamesa dampfi-Gr.
Diamesa insignipes
Diamesa latitarsis
Diamesa latitarsis-Gr.
Diamesa minor-Gr.
Diamesa permacer
Diamesa thienemanni
Diamesa cf. *thienemanni*
Diamesa zernyi-Gr.
Diamesa sp.
Diamesa sp. 2
Diamesinae cf. thomasi
Diamesa sp. 1
Diamesinae g. sp.
Diamesini g. sp.
Diplocladius cultriger
Eudactylocladius sp.
Eukiefferiella cf. *brevicalcar*
Eukiefferiella brevicalcar
Eukiefferiella brevicalcar-Gr.
Eukiefferiella cf. *fuldensis*
Eukiefferiella claripennis
Eukiefferiella claripennis-Agg.
Eukiefferiella claripennis-Gr.
Eukiefferiella coerulescens
Eukiefferiella devonica
Eukiefferiella devonica-Gr.
Eukiefferiella cf. *fuldensis*
Eukiefferiella fittkani
Eukiefferiella fuldensis
Eukiefferiella gracei
Eukiefferiella gracei-Gr.
Eukiefferiella lobifera
Eukiefferiella minor
Eukiefferiella minor-Gr.
Eukiefferiella minor/fittkani
Eukiefferiella pseudomon.-GR.
Eukiefferiella similis
Eukiefferiella sp.
Euorthocladius frigidus
Euorthocladius fuscimanus
Euorthocladius luteipes
Euorthocladius rivicola
Euorthocladius rivicola/luteipes
Euorthocladius rivicola/thienem.
Euorthocladius rivulorum
Euorthocladius thienemanni
Euorthocladius sp.
Euorthocladius sp. 4
Harnischia sp. (Gr.)
Heleniella ornaticollis
Heleniella serratosioi
Heleniella sp.
Heleniella sp. 3
Krenosmittia boreoalpina
Krenosmittia sp.
Limnophyes sp.
Macropelopia sp.
Macropelopiini g. sp.
Metriocnemus hygropetricus
Metriocnemus sp.
Micropsectra atrofasciata-Agg.
Micropsectra cf. *recurvata*
Micropsectra coracina
Micropsectra sp.
Microtendipes chloris-Gr.
Nanocladius parvulus
Nanocladius rectinervis
Natarsia sp.
Nilotanypus dubius
Odontomesa fulva
Orthocladiinae g. sp. juv.
Orthocladius cf. *fuscimanus*
Orthocladius cf. *rivicola*
Orthocladius fuscimanus
Orthocladius saxicola
Orthocladius sp.
Orthocladius sp. 1
Orthocladiini COP.
Orthocladiini g. sp. 1
Orthocladiini g. sp. 2
Orthocladiinae g. sp.
Paraboreochlus minutissimus
Paracladopelma camptolabis-Gr.
Paracricotopus niger
Parakiefferiella sp.
Parametriocnemus cf. *stylatus*
Parametriocnemus stylatus
Paratanytarsus austriacus
Paratendipes albimanus
Paratrichocladius nivalis
Paratrichocladius rufiventris
Paratrichocladius skirwithensis
Parorthocl. cf. *nudipennis*
Parorthocladius nudipennis
Pentaneurini g. sp.
Polypedilum laetum
Polypedilum laetum-Gr.
Polypedilum sp.
Potthastia longimanus
Prodiamesa olivacea
Pseudodiamesa branickii
Pseudokiefferiel. parva
Pseudosmittia sp.
Rheocricotopus effusus
Rheocricotopus fuscipes
Rheocricotopus fuscipes-Gr.
Rheocricotopus sp.
Rheotanytarsus sp.
Smittia cf. *leucopogon*
Stempellinella cf. *minor*
Stilocladius montanus
Symposiocladius lignicola
Tanypodinae g. sp.
Tanytarsini g. sp.
Thienemanniella sp.
Thienemannimyia sp. (Gr.)
Trissopelopia cf. *longimana*
Tvetenia bavarica
Tvetenia calvescens
Tvetenia discoloripes
Tvetenia sp.
Zavrelimyia signatipennis
Other Diptera:
Anopheles sp.
Atalantinae g. sp.
Atalanta sp.
Antocha sp.
Atherix ibis
Berdeniella sp.
Bezzia sp.
Ceratopogonidae g. sp.
Clinoceratinae g. sp.
Dicranota sp.
Dira sp.
Forcipomyia sp.
Hemerodromya sp.
Hemerodromyinae g. sp.
Limoniinae g. sp.
Limoniinae g. sp. 1
Limoniinae g. sp. 2
Limoniinae g. sp. 3
Limoniinae g. sp. 4
Limoniinae g. sp. 5
Liponeura cordata
Liponeura cordata/decipiens
Liponeura decipiens
Liponeura minor
Liponeura sp.
Nemothelus sp.
Oxycera pigmea
Oxycera sp.
Pericoma cf. *canescens*
Pericoma sp.
Psychodidae g. sp.
Stratiomyidae g. sp.
Thaumalea sp.
Tipulidae g. sp.
Tipulinae g. sp.
Trichocera g. sp.
Wiedemannia sp.

only about 40 taxa were restricted to drift samples (Moog & Heinisch 1991).

The Chironomidae, although not constituting a large portion of the benthic biomass, dominate the species composition of the Wagrainer Ache. A great number of them were recorded in Austria only as exceptions, e.g. *Paraboreochlus minutissimus, Boreoheptagyia* spp., the Tanypodinae *Natarsia* sp., *Trissopelopia* cf. *longimana, Zavrelimyia Nanocladius parvulus. Micropsectra auvergnensis* is new to the Austrian fauna. These species mentioned are living mainly in oligosaprobic crenal and epirhithral zones. Besides a number of quite euryoecic species (e.g. *Eukiefferiella claripennis, Paratrichocladius rufiventris, Prodiamesa olivacea, Rheocricotopus fuscipes*, and *Tvetenia calvescens*), many species are highly specialized due to the richness of the microhabitats. *Boreoheptagyia* spp., for example dwell in the spray zone. *Pseudokiefferiella parva* and *Stilocladius montanus*, as a rule, live in crystalline regions and therefore occur in the Central Alps (Rossaro 1983).

After the dipteran taxa, the Plecoptera, the Trichoptera and the Ephemeroptera followed in frequency. Within these groups, two species dominated quantitatively, the trichopteran species, *Allogamus auricollis*, the life cycle of which will be discussed, and the mayfly larvae, *Baetis alpinus*.

Choriotope dominance structure

The dominance structure and species composition of lotic communities can be separated into assemblages of three choriotopes: The "stone fauna" (litho-rheophile biocoenosis), the fauna of algal-covered cobbles and boulders (lithophytal biocoenosis), and the "rock fauna" (megalitho-rheophile biocoenosis). The lenitic communities are restricted to sand and gravel fauna (akalo-psammo-rheophile biocoenosis).

"Stone fauna" (litho-rheophile biocoenosis)

The dominating species, due to the abundance of the litho-rheophile biocoenosis, are *Baetis alpinus* (total average of individual numbers dominance 12 %), *Rhithrogena hybrida* Gr. (5 %), *Rhabdiopteryx alpina* (2.5 %), *Leuctra* spp. (21 %), *Allogamus auricollis* (27.5 %), *Rhyacophila torrentium* (2 %), *Diamesa cinerella-zernyi*-Gr. (4 %), *Orthocladius rivicola* (11 %), and *Orthocladius frigidus* (11 %). Due to the biomass *Baetis alpinus* and *Allogamus auricollis* dominate. The live cycle of *Baetis alpinus* was not analysed in detail, but the occurrence of emerging individuals indicates a univoltine cycle (Moog & Heinisch1991), comparable to the findings of Weichselbaumer (1984) and Ritter (1985) from comparable geologic sites in Tirol.

Table 4. Taxa recorded among systematic groups within choriotopes.

	Total	Drift	Lithal	Megalithal	Psammal
Oligochaeta	12	6	10	–	–
Ephemeroptera	16	7	12	6	7
Plecoptera	40	15	34	11	7
Coleoptera	4	2	3	1	–
Trichoptera	23	18	16	13	8
Simuliidae	9	5	5	5	3
Chironomidae	165	90	116	71	54
Diptera remaining	37	25	26	12	18
Others remaining	8	3	6	4	1

The fauna of algal covered-cobbles and boulders (lithophytal biocoenosis)

The fauna of the *Hydrurus*-covered boulders are dominantly *Baetis alpinus* (16 %), *Protonemura* spp. (2 %), *Allogamus auricollis* (4 %), a *Diamesa* community (31 %) – (*D. cinerella, D. zernyi, D. dampfi, Pseudodiamesa branickii*), *Eukiefferiella devonica*-Gr. (3 %), *E. minor*-Gr. (6 %), and *Orthocladius rivicola* (5 %). These findings are in good coincidence with the *Hydrurus*-biocoenoses described by other authors (Kawecka, Kownacka & Kownacki 1971, Lehmann 1971, Serra-Tosio 1973).

"Rock fauna" (megalitho-rheophile biocoenosis)

The dominant species among boulders within those areas characterized by swift currents and without dense algal aufwuchs are *Liponeura cordata, Liponeura decipiens, Simulium argyreatum*, and *Simulium variegatum*. These animals show an extremely clumped distribution. Because of too small replicates, no estimation of the relative proportion of abundance or biomass is given.

Sand- and gravel fauna (akalo-psammo-rheophile biocoenosis)

Out of 107 taxa totally recorded from the sand and gravel areas, only five were constantly dominant: *Stylodrilus heringianus* (8 %), *Leuctra* spp. (4 %), *Allogamus auricollis* (25 %), *Pseudodiamesa branickii* (26 %), *Polypedilum laetum*-Gr. (3 %) and Limoniinae g. sp. (7 %). In facultatively larger numbers appeared *Choloroperla* sp., *Heleniella* sp., and *Micropsectra* sp.

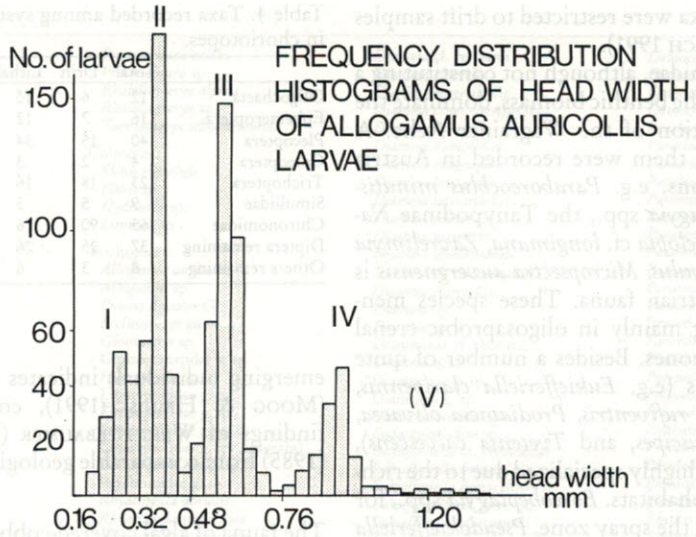

Fig. 2. Frequency distribution histograms of head width of *Allogamus auricollis* larvae.

A. auricollis recruits about a quarter of the mean annual individual abundance relative to the biomass. During the first two months after hatching, the *Allogamus* individuals dominate the biomass to an extent between 52 % (November 1985) and 72 % (November 1984). With the exception of the first instar larvae, the major part of the *A. auricollis* population is distributed within the psammal areas of the river bottom. This species, shredding medium to fine particles, lives mainly at the surface of psammal patches where the slow current allows the sedimentation of their favorite nourishment particles. This finding coincides well with the observations made by WARINGER (1989), who determined that *A. auricollis* should be restricted to areas of the stream bed where currents are below 30 cm · s^{-1}.

For instar analysis, the maximum head width was measured to the nearest 0.01 mm. The first four larval instars could be well defined with respect to their head widths; too few instars 5 were found for analysis (Fig. 2). The head width ranges are in good agreement with data reported from populations of an Austrian clean calcareous mountain brook (Lunzer Seebach, WARINGER 1989). Therefore, the head width-instar-relationship of WARINGER (1989) was used for the 5th instar determination. Pupae of *A. auricollis* were not found, but their emerging period could be deduced by means of the presence of adults, which occurred periodically and numerously between August and October.

The graphic analysis of instars and adults indicates clearly a 1-year life cycle (Fig. 3). The first instar larvae occur between September and November. Mainly the second and third instars are overwintering. Moulting to the last instar is completed during June and July. The seasonal distribution of abundances also indicates a univoltine cycle. High abundances are to be found during the first instars. The broad confidence limits of the mean indicate the clumped distribution of the newly hatched first and second instar larvae which are to be found very near to the egg-laying sites, just below them, or in current-protected areas among larger stones, during the first weeks of their life. During subsequent development, the abundances drop steadily due to mortality and, probably, because of leaving the distinct river bottom area.

The role of *Hydrurus foetidus*

The phytobenthos of the Wagrainer Ache is dominated by a single species: The Chrysophyceae, *Hydrurus foetidus*. This algae covers densely the upper and lateral sides of the boulders and cobbles. Another important algal-group are the Diatoms, which represent 86 taxa out of a total of 133 algal taxa, followed by the blue-greens (31 taxa), Chlo-

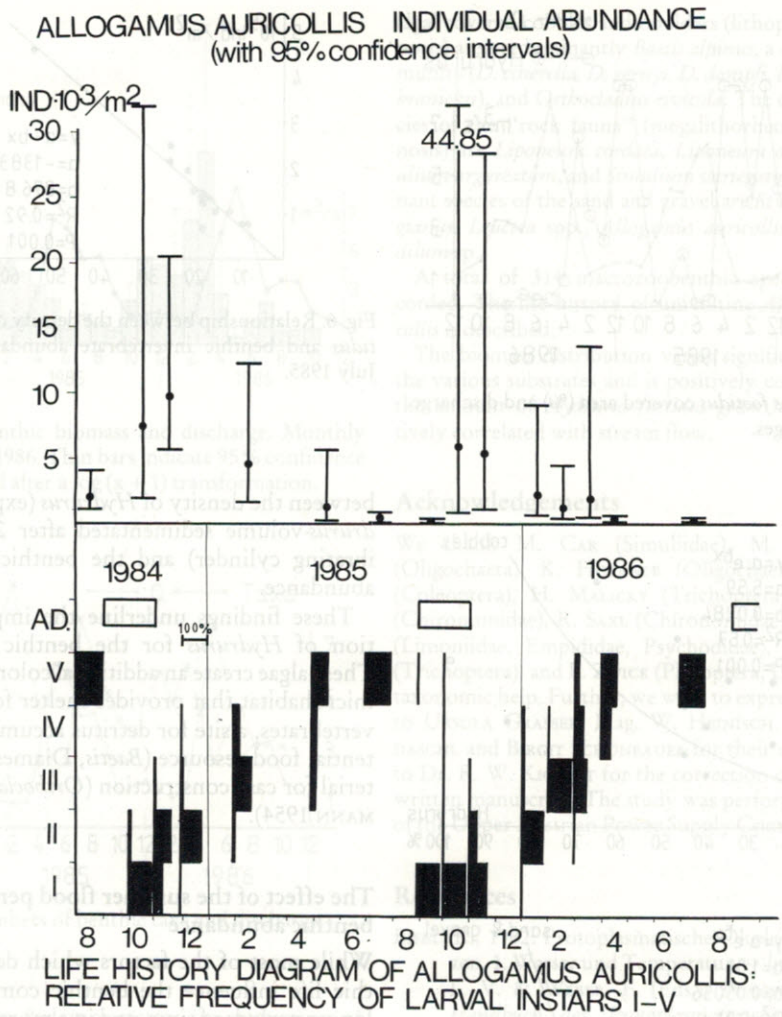

Fig. 3. Life history diagram of *Allogamus auricollis*. Relative frequency of larval instars I–V. Thin bars indicate 95 % confidence limits, calculated after a log (x + 1) transformation.

rophyceae (9), Rhodophyceae (5) and Chrysophyceae (3), (Pum pers. comm.).

Hydrurus is a cold stenotherme species which favors temperature conditions between 0.2 and 13.3 °C (Bursa 1934, Kawecka 1981). Maximal temperature tolerated is 16 °C, since at higher temperatures breathing exceeds the constitutive metabolism (Biebl 1962, Starmach 1985). Optimal growth takes place between 1.4 and 5.9 °C (Kawecka 1977).

Although *Hydrurus* favors strong water currents (Oeggl 1986), the occurrence and quantitity of this algae depends mainly on the occurrence of floods. With the exception of the two summer months of August and September, during which the higher water temperatures (14–16 °C) depress the *Hydrurus* growth, the discharge is negatively correlated with the %-share of *Hydrurus* covered areas (regression analysis shows a potential function: $y = a \cdot x^b$; $R^2 = 0.78$; $a = 57.62$; $b = -1.5$; $P = 0.001$). Fig. 4 gives the relationship between discharge and *Hydrurus* covered areas.

Regarding the seasonal benthic distribution, the *Hydrurus* density is positively correlated with the benthic biomass. The relationship between the *Hydrurus*-covered stream bottom-area (%) and the benthic biomass is exponential (Fig. 5).

Regarding the spatial benthic distribution in dependence of the *Hydrurus* density, a significant relationship between the amount of *Hydrurus* and

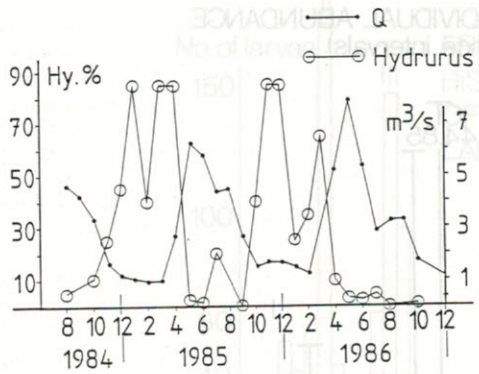

Fig. 4. *Hydrurus foetidus* covered area (%) and discharge. Monthly averages.

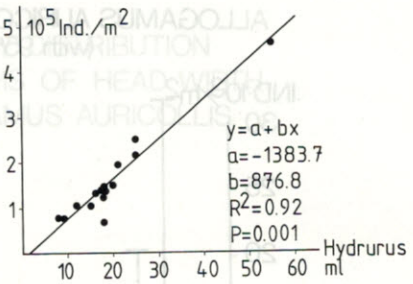

Fig. 6. Relationship between the density of *Hydrurus foetidus* and benthic invertebrate abundance. Boulders. July 1985.

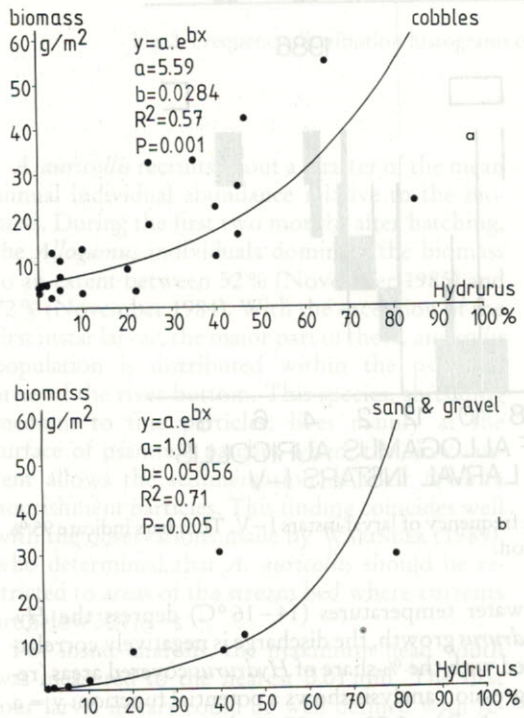

Fig. 5. Relationship between the *Hydrurus foetidus* covered stream bottom area (%) and the benthic biomass. a) cobbles, b) sand and gravel. Monthly averages.

the benthic abundance could always be found. To underline the significance of *Hydrurus* on the benthic abundance at *Hydrurus* covered boulders, the situation from 8/7/1985 is taken as an example in Fig. 6. The 15 samples show a linear relationship between the density of *Hydrurus* (expressed as *Hydrurus*-volume sedimentated after 24 h in a calibrating cylinder) and the benthic invertebrate abundance.

These findings underline the important function of *Hydrurus* for the benthic community. These algae create an additional colonizing space, a microhabitat that provides shelter for benthic invertebrates, a site for detritus accumulation, a potential food resource (*Baetis*, Diamesini), and material for case construction (*Orthocladius*, Thienemann 1954).

The effect of the summer flood period on benthic abundance

While most of the factors which determine benthic life influence the benthic community over longer periods of time, and in a more or less inconspicuous way, the effects of a flood abruptly alter the benthic composition and its abundance. In most cases, spates decrease the benthic fauna (e.g. Hynes 1970), by "washing out" (Bishop & Hynes 1969). In contrast to repeated artificially induced floods, which cause permanent faunal damage (e.g. Bretschko & Moog 1989), the effects of natural spates are to be seen positively and have an important regulating function in stream ecology (e.g. Lehmkuhl & Anderson 1972).

Fig. 7 shows a yearly cycle between high faunal biomasses, mainly dependent on the amount of *Hydrurus foetidus*, during low water flow conditions and an algal and invertebrate breakdown during the summer flood period. The regression analysis between benthic biomass and monthly means of discharge shows a potential relationship with an R^2 of 0.54 (n = 21; a = 26.80; b = −0.992;

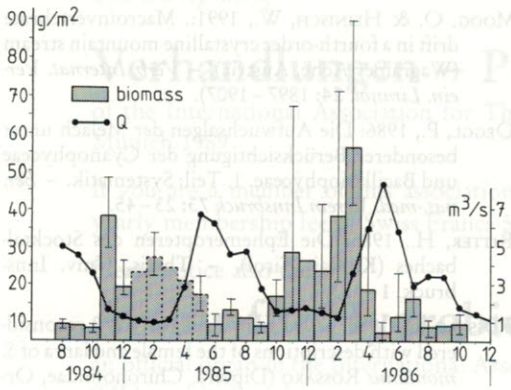

Fig. 7. Total benthic biomass and discharge. Monthly averages 1984 – 1986. Thin bars indicate 95 % confidence limits, calculated after a log (x + 1) transformation.

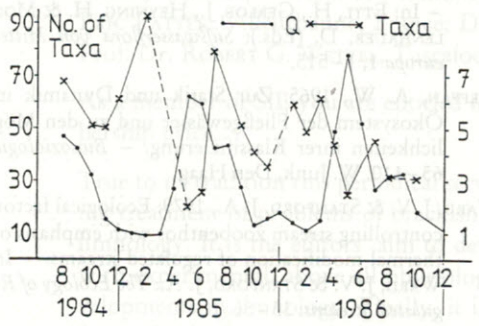

Fig. 8. Total numbers of benthic taxa and discharge.

P = 0.001). Fig. 8 demonstrates the reduction of species number during the floods.

The data obtained at the Wagrainer Ache document that the yearly floods between late spring and summer significantly alter the benthic fauna, both in abundance (biomass) and in species richness.

Summary

The bed sediments of the Wagrainer Ache consist of three main choriotopes: Psammal and akal (sand and gravel), lithal (cobble), and megalithal (boulders). The macrozoobenthic biocoenosis of these choriotopes differ significantly both in abundance and assemblages. The dominant species of the litho-rheophil biocoenosis are *Baetis alpinus, Rhithrogena hybrida* Gr., *Rhabdiopteryx alpina, Leuctra* spp., *Allogamus auricollis, Rhyacophila torrentium, Diamesa cinerella-zernyi*-Gr., *Orthocladius rivicola*, and *Orthocladius frigidus*. The fauna of algal covered cobbles and boulders (lithophytal biocoenosis) are predominantly *Baetis alpinus*, a *Diamesa* community (*D. cinerella, D. zernyi, D. dampfi, Pseudodiamesa branickii*), and *Orthocladius rivicola*. The dominant species of the "rock fauna" (megalithorheophile biocoenosis) are *Liponeura cordata, Liponeura decipiens, Simulium argyreatum*, and *Simulium variegatum*. The dominant species of the sand and gravel are *Stylodrilus heringianus, Leuctra* spp., *Allogamus auricollis*, and *Polypedilum* sp.

A total of 314 macrozoobenthic species were recorded. The life history of univoltine *Allogamus auricollis* is described.

The biomass distribution varies significantly among the various substrates and is positively correlated with the amount of *Hydrurus foetidus* growth and is negatively correlated with stream flow.

Acknowledgements

We thank M. Car (Simuliidae), M. Hochreiter (Oligochaeta), K. Hoerner (Oligochaeta), M. Jäch (Coleoptera), H. Malicky (Trichoptera), H. Ritter (Chironomidae), R. Saxl (Chironomidae), R. Wagner (Limoniidae, Empididae, Psychodidae), J. Waringer (Trichoptera), and P. Zwick (Plecoptera, Liponeura) for taxonomic help. Further, we want to express our thanks to Ursula Grasser, Mag. W. Heinisch, Helga Raudaschl and Birgit Schönbauer for their assistance and to Dr. R. W. Kickert for the correction of the English written manuscript. The study was performed by order of the Upper Austrian Power Supply Company (OKA).

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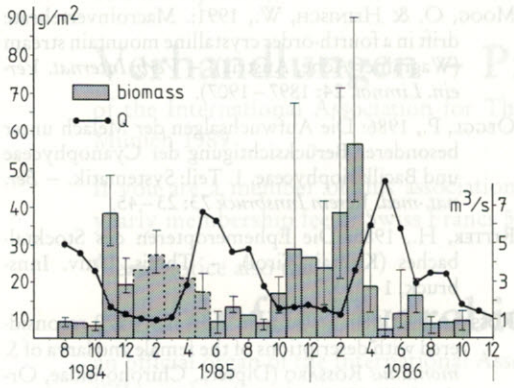

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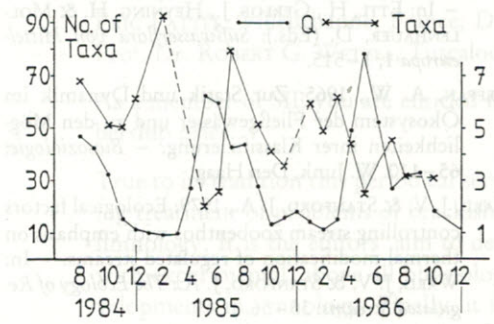

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